Mechanisms of resistance of freshwater macrophytes to herbivory by invasive juvenile common carp

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SUMMARY

1. Herbivory on freshwater macrophytes has been assumed to be insignificant and rare. More recent evidence suggests herbivory is common and the impact of invasive invertebrate herbivores can be substantial. However, little is known about consumption of macrophytes by fish.

2. We performed a series of feeding assays, based on the consumption by common carp (*Cyprinus carpio*), to determine if any mechanisms of resistance, structural or chemical, were present in five species of macrophytes (*Stuckenia pectinata*, *Typha latifolia*, *Scirpus validus*, *Chara aspera* and *Ceratophyllum demersum*).

3. Carp consumed more fresh whole plant tissue of *C. aspera* than any other macrophyte, suggesting a lack of structural or chemical deterrents. *Typha latifolia*, *S. validus* and *C. demersum* were consumed least as whole plants, but consumption increased when they were offered in pellet form suggesting structural defence. Crude chemical extracts from *S. pectinata* significantly reduced consumption of pellets by carp. Thus, plant chemistry and structure both deterred feeding by carp.

4. Experiments that focus on theory are common but their application to managing landscapes is substantially lacking. Our results provide a basis for recommending plants to be used in restoring larval habitat refugia with the aim of increasing the probability for long-term recovery of an endangered species. Thus, this paper is an example of how experiments that tie theory to application are important for practical applications and for continued testing of theory.

5. We suggest that macrophyte–herbivore interactions play an integral part in aquatic food webs and may be as important in freshwater communities as in marine and terrestrial systems.

Keywords: chemical deterrents, common carp *Cyprinus carpio*, defence mechanisms, macrophytes, plant–herbivore interactions

Introduction

In aquatic systems, macrophytes are important contributors to food webs through detrital pathways, which increase microbial conditioning and detritus nutrient content (Newman, 1991). Aquatic macrophytes are also essential to many invertebrate and some vertebrate species as a refugium from predation, substrate for spawning and as food (Hutchinson, 1975). While herbivory on freshwater aquatic macrophytes historically was assumed to be insignificant and rare (Hutchinson, 1975, 1981), reviews by Lodge (1991) and Newman (1991) signalled a paradigm shift, and current research provides examples of substantial impacts on macrophytes by both vertebrate and invertebrate herbivores (Lodge & Lorman, 1987;

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Lodge, 1991; Bolster *et al.*, 1998; Cronin, 1998; Lodge *et al.*, 1998; Bonar, Bolding & Devins, 2002; Miller & Crowl, 2006). Herbivory may become more pronounced when non-native herbivores are introduced, suggesting that primary production of macrophytes in freshwater ecosystems can be impacted both ecologically and economically by exotic species (Allan & Flecker, 1993; Zambrano, Scheffer & Martinez-Ramos, 2001; Tapia & Zambrano, 2003; Rosenthal *et al.*, 2005; Parker, Burkepile & Hay, 2006). Exotic generalist herbivores, such as crayfish (*Orconectes rusticus*), can substantially reduce macrophyte abundance through consumption, destruction and increased turbidity (Lodge & Lorman, 1987; Lodge, 1991; Cronin, 1998).

Common carp (*Cyprinus carpio* L.), a generalist fish introduced to Utah Lake (Utah, U.S.A.) in 1888, have caused considerable damage to the macrophytes and endemic fishes of this freshwater ecosystem (Heckman, Thompson & White, 1981). Vegetation maps from the mid-1800s, prior to carp introduction, show the lake covered with extensive macrophyte communities (National Archives Microfilm Publications [RG48:Utah, 1850–1902 'M428, 6 rolls']; Brotherson, 1981). Today these communities are virtually nonexistent, and only three macrophytes remain in Utah Lake; one submergent, *Stuckenia pectinata* B. (formerly known as *Potamogeton pectinatus* L.), and two emergents, *Typha latifolia* L. and *Scirpus validus* L. *Ceratophyllum demersum* L. has been extirpated entirely and *Chara aspera* L. occurs only in tributaries running into the lake.

Macrophytes provide essential structural refugia for larval fish and invertebrates (Hutchinson, 1975; Lodge, 1991; Newman, 1991; Persson & Crowder, 1998). Loss of refugia is the main source of mortality for larval and juvenile endangered june suckers (*Chasmistes liorus* L.), a remnant species from the late Pleistocene that lived in lake Bonneville; Utah Lake and the Great Salt Lake (Utah, U.S.A.) were once a part of lake Bonneville (Crowl, Thomas & Vinson, 1998). Due to predation by non-native species, habitat degradation, and the lack of structural habitat to serve as refugium, long-term recovery of the june sucker in Utah Lake is not likely unless managers can revegetate the lake with refugia resistant to carp.

Hutchinson (1975) suggested freshwater macrophytes are not consumed by herbivores because they are less nutritious than other foods. However, Lodge (1991), Lodge *et al.* (1998) and Burks & Lodge (2002)

concluded that there is no evidence macrophytes have lower food quality than terrestrial plants or algae; although, they are lower in quality than terrestrial broad-leaf herbs. Despite limited data, many scientists now agree the probable explanation for the low rates of herbivory on macrophytes is the presence of deterrent secondary compounds (Otto & Stevenson, 1981; Ostrofsky & Zettler, 1986; Newman, 1990, 1991; Newman, Kerfoot & Hanscom, 1996; Kubanek *et al.*, 2000; Cronin *et al.*, 2002).

Ehrlich & Raven (1965) were the first to propose that plants evolved secondary chemicals in part as defences against herbivory. The study of secondary metabolites, which began in the 1800s, focused on terrestrial plants and animals, and showed that several defence mechanisms have evolved in terrestrial plants that reduce herbivory (Rhoades, 1979; Fox, 1981; Coley, Bryant & Chapin, 1985; Feeny, 1992), including thorns and spines. More recent studies have advanced our knowledge of the chemical ecology of marine systems considerably (Hay & Fenical, 1988; Hay, 1996), and the notion that chemical defences are unimportant in macrophytes (Ostrofsky & Zettler, 1986) is now being revised to reflect more current views that freshwater herbivory is widespread (Lodge *et al.*, 1998; Burks & Lodge, 2002). These views call for better mechanistic understanding of this area of ecology (Lodge *et al.*, 1998).

We performed a series of assays to determine whether structural, chemical or nutritional elements deterred consumption of macrophytes by carp. Each macrophyte species was further analysed for toughness, ratio of carbon to nitrogen, soluble protein and phenolic content to assess whether any of these parameters were correlated with consumption of macrophytes by carp. Our aim was to understand the mechanism of resistance of each macrophyte and thereby to offer managers a suitable suite of plants to be used in restoring habitat in Utah Lake and other areas with invasive carp.

Methods

Feeding assays

Utah Lake (40°10′58″N × 111°43′46″W) is located in north-central Utah. The lake is large and shallow with a surface area of approximately 388 km², a mean depth of 2.9 m and a maximum depth of 4.2 m at

highest lake elevation. It is highly eutrophic, turbid (average Secchi depth 12 cm), slightly saline (average salinity 1.5 g L^{-1}), and dominated by mud substrate with some sand and gravel in littoral areas. Algal blooms occur in several areas of the lake during the summer. Non-native carp (*C. carpio*), white bass (*Morone chysops* L.), and walleye (*Stizostedion vitreum* L.) are the predominant fish species. Utah Lake's main tributaries are the Provo and Spanish Fork rivers, with other smaller tributaries dominated by nutrient-rich irrigation return flows.

In the summer of 2003, we collected three species of macrophytes from Utah Lake: *S. pectinata*, *T. latifolia* and *S. validus* (Fassett, 1957). The macrophyte *C. aspera* was collected from the Provo River, a tributary of Utah Lake. *Ceratophyllum demersum*, which has been extirpated from Utah Lake and is no longer found locally, was purchased from a local pet store. All plants, once acquired (June 2003), were planted at the Millville Aquatic Research Laboratory (Millville, Utah, U.S.A.) where they were reared in 189-L aquaria randomly assigned under four 100 W growing lights.

Carp were collected from experimental ponds at the Millville Aquatic Research Laboratory, where eggs from adult Utah Lake carp were reared to the size class of the age 0 fish found in Utah Lake. The current carp population of Utah Lake is estimated to be >100 million with a minimum of 5.9 million adults, 13 million of age 1 fish and 90 million age 0 (Valdez, Widmer & Kehmeir, 2006). All carp used in the experiments were first year juveniles from 4.0 to 6.5 cm in length with a mean ± SE length of 5.1 ± 0.13 cm. Live carp were randomly assigned to treatment aquaria and acclimated for each series of assays.

We used 25 189-L, 127 × 38 × 58 cm, aquaria to house individual carp. For each assay, a new fish was randomly assigned to an aquarium; no fish was used in more than one assay to prevent order effects (Steinberg, 1985; Roa, 1992). In addition, assignments to treatments were randomized and fish were allowed to acclimate in treatment aquaria for 3 days before we performed an assay. Water in all aquaria was filtered water (16–19 °C) which was shut off each day for feeding, whether in a treatment or as regular feeding, and water in each treatment aquaria was changed completely prior to each assay.

To prevent hunger stress during assays, carp were fed approximately 0.10 g commercial koi food (Crude fibre max 4.5%, Crude fat minimum 2.5%, Crude protein minimum 33%) daily 1 h before and after each assay. This is the average amount of food a fish consumes in a 5-min period (per feeding instructions Wardley Pond Ten brand; Brooklands V.I.P Pet Products, New Plymouth, New Zealand) and was the amount of food fed to all carp daily. Each feeding assay occurred for a 2-h period (9:00–11:00 hours each day) and was repeated for three consecutive days. New assays each week, corresponding to each of four treatments, were performed over consecutive weeks.

We performed a series of five assays to determine if plant structure and/or chemical composition reduced consumption of freshwater macrophytes by carp. As assays were performed over 4 weeks instead of simultaneously, five of the 25 aquaria (one carp per aquaria) were used to control for potential time effects. New carp were added each week to these five aquaria and fed approximately 0.25 g (0.248–0.253 range) wet mass whole plant (one plant species per carp) to determine if the rate of consumption changed over the duration of the experiment. We used PROC REG in SAS 9.0 (SAS Inst., Cary, NC, U.S.A.) to assess changes in the slope between whole plant consumption and week number for each plant species.

For the first assay, we used fresh plant tissue. In this no-choice assay, each of the five species of plants was added to five different aquaria, with five replicates for each species for a total of 25 aquariums. Each plant piece was blotted using a paper towel to remove excess water and weighed before and after the assay. Roa (1992) suggests performing all assays with autogenic controls doubling the number of tanks needed to perform a single assay. Our data suggest a different approach can be taken dependent on the organism and plant species in question. In our case, an autogenic control was unnecessary because our preliminary data showed no significant difference in plant wet-weight over a 2-h period at 17 °C in any of the plant species (*t*-test: wet-mass before versus after; d.f. = 10, *P* = 0.77). In addition, we used plant pieces that were approximately equivalent in mass to those used in the artificial food assays (described below). Consumption was estimated as the difference in plant wet-mass before and after each assay.

For the second assay, we assessed if plant structure and/or chemical composition influenced food choice. To do so, we made artificial food pellets that isolated structural components of plants from chemical

components (Hay, Kappel & Fenical, 1994; Bolster *et al.*, 1998). To control for plant structure, we made pellets with lyophilized and finely ground plant material. We prepared the pelletized food by mixing 10 mL of water with 0.50 g of agar which was heated in a microwave oven for approximately 40 s until boiling. This mixture was stirred and then poured into 5 mL of cold water containing 1.5 g of the desired ground (lyophilized) plant and then stirred again to assure uniformity. This agar-based food was poured into a mould and smoothed to a uniform thickness with a razor blade (Hay *et al.*, 1994; Bolster *et al.*, 1998). After solidifying, agar-based food was cut into $3 \times 3 \times 2$ mm pellets that did not exceed juvenile carp gape (3.5–4.5 mm). Each pellet contained material equalling 0.0625 g of food or extract material per pellet.

For the third and fourth assays, we determined whether water-soluble (extracted with methanol/dicloromethane) or non-water-soluble (extracted with diethyl ether) crude chemical extracts from lyophilized plants, when incorporated into palatable foods, affected consumption. Each assay was carried out separately. Extraction followed the methods described by Bolster *et al.* (1998). We used chemical extracts from each plant species (extracted from 1.5 g lyophilized plant material), which were then added to an artificial food mixture (1.5 g lyophilized broccoli and lettuce, 10 mL water, 5 mL crude extract) and again formed into pellets. The palatable agar-based food made of lyophilized broccoli and lettuce is referred to as 'broc-let' (Hay *et al.*, 1994; Bolster *et al.*, 1998). Finally, a fifth assay provided baseline data for consumption of artificial food without any macrophyte extract (1.5 g broc-let, 10 mL water, 5 mL cold water).

In all trials, we used four replicate assays for each plant species in addition to one control for a time effect as described above. Each trial lasted for 2 h, at the same time each day for three consecutive days. New pellets and whole plant pieces were offered each day. In assays with pellets, we determined the number of pellets each fish consumed, and thus grams of each species eaten (each pellet contained 0.0625 g of lyophilized plant material); four pellets of one species were offered to each fish. We used an equal amount of plant material per pellet to keep treatments consistent on a lyophilized weight basis rather than dry mass/volume. This ensured fish were

fed equal amounts of each plant and allowed us to feed each fish exact amounts of supplemental koi food daily. Thus, we allowed the fish to regulate their intakes of the foods. Herbivores regulate the amount of plant material ingested based on their individual needs (Provenza *et al.*, 2003).

We computed the mean consumption by each fish over the 3 days for each assay. Differences in consumption based on species and treatment were analysed using a completely randomized block design two-way ANOVA with consumption as the main effect and plant species and food preparation as the explanatory variables. We also partitioned variability among fish and within fish and subsamples to assess individual fish-effects in our treatments. Analysis of data was conducted using the PROC MIXED procedure of SAS version 9.0. Data met assumptions for homogeneity of variance and normality.

Plant traits

We measured the following plant traits during the course of our experiment to determine if differences existed among the macrophyte species: toughness, carbon, nitrogen, protein and phenolic content. Data were analysed using plant traits as the explanatory variable and whole plant consumption as the response using multiple linear regression (SAS 9.0). To determine toughness we measured the mass (g) required to penetrate fresh leaves using a penetrometer (commonly used to measure fruit firmness by measuring the amount of weight needed to puncture through the skin with a needle). We analysed the carbon and nitrogen content of the fresh plant tissue using a Leko CHN analyzer (Leko, St. Joseph, MI, U.S.A.). Soluble protein content was determined for lyophilized and ground plants using the Bradford method (Bradford, 1976; Bolster *et al.*, 1998). Phenolic content was determined using a modified Folin–Ciocalteu method where absorbances were measured spectrophotometrically at 765 nm and compared with those of a standard curve for gallic acid (Folin & Ciocalteu, 1927 as modified by Bolster *et al.*, 1998).

Results

Consumption of each plant differed by treatment. Carp consumed more *C. aspera*, but less *T. latifolia*, *S. validus* and *C. demersum*, as fresh whole plant tissue
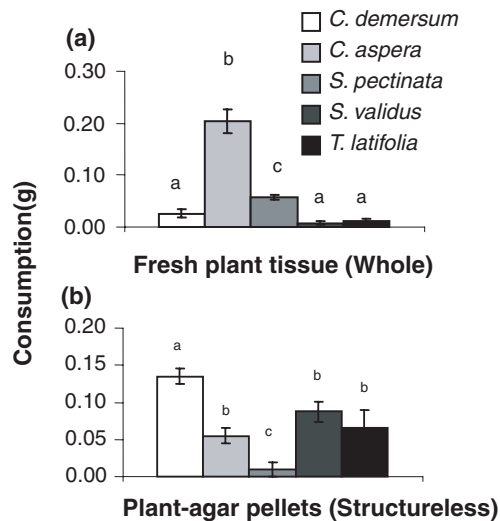
Fig. 1 Results from whole plant and structureless feeding assays based on mean consumption of each macrophyte species: (a) fresh plant tissue (0.25 g) (b) lyophilized and finely ground tissue (0.0625 g each pellet) mixed with an agar base. Bars represent ±1 SE and letters above each bar represent statistical differences between species based on consumption.
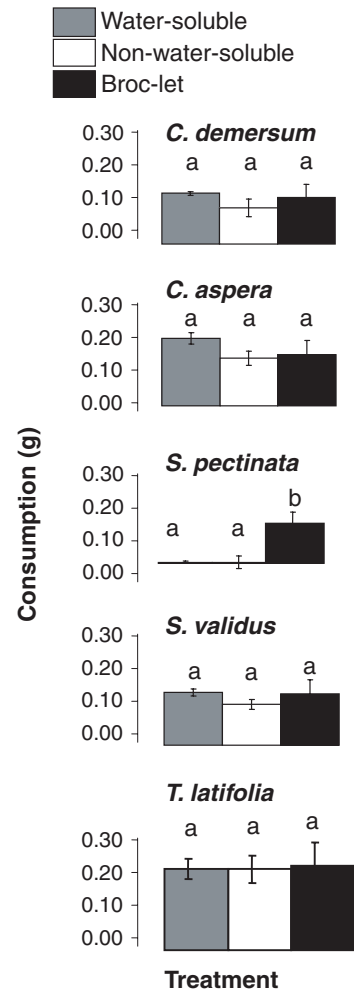

Fig. 2 Effects of water-soluble and non-water-soluble crude extracts from each macrophyte species on consumption by common carp. Crude extracts from each species were incorporated into a broc-let mixture (0.0625 g each pellet) and compared with a broc-let only assay. Bars represent ±1 SE and letters above each bar represent statistical differences between species based on consumption.

(Fig. 1a). However, when we removed plant structure and fed carp the same plants in pellet form, *C. demersum* was consumed most, and *S. pectinata* was consumed least (Fig. 1b). There were no differences in consumption among *C. aspera*, *T. latifolia* and *S. validus*.

Water-soluble and non-water-soluble (lipophilic) extracts from *S. pectinata* were consumed least by carp relative to all other plants and the broc-let mixture (Fig. 2). Although *S. pectinata* was consumed least in both extract assays, no significant difference between extracts was found; both water-soluble and non-water-soluble (lipophilic) extracts from *S. pectinata* reduced pellet consumption by carp. Neither water-soluble nor lipophilic extracts from *C. aspera*, *C. demersum*, *S. validus* or *T. latifolia* significantly affected consumption by carp.

Consumption of *C. demersum* ($P = 0.49$), *C. aspera* ($P = 0.64$), *S. pectinata* ($P = 0.38$), *S. validus* ($P = 0.54$), and *T. latifolia* ($P = 0.33$) did not change throughout the experiment in the control group. Therefore, differences in consumption rates were because of treatment effects and not because of time effects. We also tested for temporal (within fish) variance in the amount of food consumed based on plant and treatment by performing the same assay with the same fish for 3 days in a row. We conducted new

assays each week with different fish, and again, no significant differences were detected.

Differences in the physical and chemical characteristics of plants were correlated with food consumption by carp. Based on multiple linear regression, consumption of whole plant tissue was positively correlated with total phenolic content and negatively correlated with carbon content ($R = 0.73$, d.f. = 24, $P < 0.0001$). Although stem and leaf tissue toughness were strongly correlated with consumption, they were removed because of strong multicollinearity with the other variables, specifically carbon content. In addition, the toughness levels of *T. latifolia* and

Table 1 Differences in plant quality among macrophyte species used in feeding assays*

Plant	Tissue toughness (g) stem (s) leaf (l) ($n = 15$)	Carbon % dry mass ($n = 5$)	Nitrogen % dry mass ($n = 5$)	C : N	Total phenolic content mg 100 mL^{-1} (dry mass) ($n = 10$)	Soluble protein mg 100 mL^{-1} (dry mass) ($n = 3$)
Ceratophyllum demersum	299 ± 75 (s) 76 ± 19 (l)	37.2 ± 0.17	3.5 ± 0.08	10.6	4.3 ± 1.3	0.10 ± 0.04
Stuckenia pectinata	362 ± 90 (s) 63 ± 16 (l)	34.8 ± 0.29	1.3 ± 0.11	27.0	4.9 ± 1.5	0.20 ± 0.12
Scirpus validus	>500 ± 125 (s) >500 ± 125 (l)	38.6 ± 0.33	1.3 ± 0.11	28.9	6.7 ± 2.0	0.19 ± 0.11
Typha latifolia	>500 ± 125 (s) >500 ± 125 (l)	38.9 ± 0.29	0.8 ± 0.11	47.1	7.0 ± 2.1	0.15 ± 0.08
Chara aspera	0.05 ± 0.01 (s) 0.10 ± 0.02 (l)	20.7 ± 0.13	1.1 ± 0.07	18.3	3.3 ± 1.0	0.13 ± 0.06
Broc-let	N/A	39.5 ± 0.10	4.1 ± 0.01	9.6	10.3 ± 3.1	0.28 ± 0.17

*All analyses were performed on new plant material; no plant was used more than once for any of the above tests. All values ±1 SE.

S. validus were >500 g, which was higher than the recording capabilities of our penetrometer. *Typha latifolia* and *S. validus* had the highest levels of carbon and the leaves and the stems were toughest compared with other plants (Table 1). *Ceratophyllum demersum* and *S. pectinata* were similar in carbon content and both had three times tougher stems than leaves; *C. aspera* had the lowest carbon content and virtually no toughness (Table 1). Although *C. aspera* was the most highly consumed plant in whole-plant assays, it ranked lowest in per cent carbon and was low in nitrogen and soluble protein. Yet, despite its lack of nutritional quality it remained relatively palatable possibly due to its low toughness and phenolic content and lack of chemical defence (Table 1). *Typha latifolia*, *S. validus* and *P. pectinata* all had high carbon, low nitrogen levels and were highest in phenolic content (Table 1). Protein, nitrogen content and C : N were not significantly correlated with whole plant consumption.

Discussion

Plant structure and chemical composition both affected consumption of macrophytes by common carp, a vertebrate generalist herbivore. *Typha latifolia*, *S. validus* and *C. demersum* were consumed less as whole plants but more as pellets (Fig. 1). These plants were also the highest in carbon content and the toughest, suggesting their structure reduced herbivory (Table 1). Consumption of *C. demersum* increased in all pellet assays, suggesting structure, rather than a chemical deterrent, reduced consumption. However, we did not find a clear increase in consumption of all plants in the structureless pellet assays (Fig. 1). Some plants were actually consumed less as agar pellets (structureless assay) than as whole plants, suggesting either that the lyopholization process may degrade cells and release otherwise contained secondary metabolite fractions or that nutritional changes occurred during the lyophilizing process (Hay *et al.*, 1994; Centrulo & Hay, 2000). In all assays, *S. pectinata* was consumed infrequently, suggesting the presence of deterrent chemicals in both the water-soluble and non-water-soluble extracts (Fig. 2). Thus, plant chemistry and structure had both deterrent and stimulatory effects on the feeding behaviour of carp. Further fractionation and additional feeding assays are necessary to determine which compounds deter herbivory and whether these compounds differ from terrestrial compounds.

Herbivores typically select plants that have the highest nutritional quality (Hay *et al.*, 1994; Cruz-Rivera & Hay, 2000). Interestingly both *S. validus* and *S. pectinata* had the highest levels of soluble protein and similar C : N ratios as well as percentages of carbon and nitrogen, suggesting that they were the most nutritious (Table 1). Nonetheless, they were protected by two different mechanisms. *Scripus validus* is tough and carbon rich, while *S. pectinata* appears to have chemical deterrents. Thus, plants with higher nutritional content were more highly defended structurally or chemically (Cronin & Hay, 1996a,b).

Carbon is always more abundant than nitrogen in plant tissue, so herbivores are more likely to be stimulated by increased nitrogen or protein quantity than by carbon. Carbon is also a large component of structure, creating tougher tissue, and a high carbon to nitrogen ratio may reduce palatability. In fact, McMahon, Hunter & Russekk-Hunter (1974) argued that herbivores require C : N ratios <17 for food to be palatable enough to consume. *Typha latifolia*, *S. validus* and *S. pectinata* all had very high C : N ratios and highest levels of carbon (Table 1). Broc-let had the lowest C : N ratio as well as the highest soluble nitrogen levels, making it the most palatable and nutritious food used in any assay. While the ratio of C : N in *C. aspera* was slightly higher than 17, it was consumed most in the whole plant assay. Thus, *C. aspera* was a palatable but less nutritious food source. The greater consumption of *C. aspera* may be due to low C : N ratio, low toughness and the apparent lack of chemical deterrents. It is also possible that daily feeding of commercial koi food high in nitrogen may have complemented the soluble carbon in *C. aspera* chemistry and thus increased intake, the two food sources providing a balance of protein and energy.

Total phenolic content does not appear to be a good indicator of chemical deterrence (Hay, 1991). In fact, our regression analysis suggests that total phenolic content is positively correlated with whole plant tissue consumption ($R = 0.73$, d.f. = 24, $P < 0.0001$). Intake of broc-let, which had the highest total phenolic content, was higher than most whole plant and agar-pellet-based macrophytes, which suggest phenols may actually increase preference in some cases. Phenols at appropriate doses can provide nutritional and health benefits in terrestrial herbivores (Provenza & Villalba, 2006). However, other factors, including % dry mass and nutrient content, could also cause this pattern.

Plant defences are herbivore-specific and may depend on handling ability and ability to withstand chemical deterrents (Lodge *et al.*, 1998). When plant pellets were offered to crayfish (*Procambarus clarkii* L.), a generalist omnivore, *T. latifolia* was preferred slightly more than *C. aspera* and *C. demersum* because of the higher nutritional quality of *T. latifolia* and the presence of an unidentified chemical stimulant (Cronin, 1998; Cronin *et al.*, 2002). Slight differences in consumption between carp and crayfish may be due to greater handling abilities of crayfish than carp;

crayfish possess claws that can easily shred plant material. Several studies indicate *S. pectinata* is an important food for waterfowl and is also heavily eaten by muskrats (*Ondatra zibethica* L.), beaver (*Castor canadensis* L.), deer (*Ococoileus* spp.) and moose (*Alces alces* L.) (Fassett, 1957; Robel, 1962). Therefore, differences in plant–herbivore interactions depend on available nutritional resources, the herbivore present and whether the herbivore has the ability to cope with the plant defence. While common carp are an invasive fish in Utah Lake, they presumably co-evolved with all but *S. validus*, as all of the other macrophytes are found in Eurasia.

Common carp can consume best the plant parts they can handle, something that is dependent on their mouth morphology. Upon senescence or death, macrophyte structural integrity is reduced (Newman, 1991; Cronin & Hay, 1996a), which may increase the ability of carp to handle and process macrophytes. While they are unable to consume plants with high tissue toughness or fibre content (Sibbing, Osse & Terlouw, 1986), this does not preclude them from consuming macrophytes in general. Adult and juvenile carp fed on the soft exposed roots of *T. latifolia* and on *C. aspera* in experimental ponds (Miller, 2004). Although ontogenetic shifts in diet frequently occur in many fish species (Osenberg, Mittlebacj & Wainwright, 1992), Yilmaz *et al.* (2003) found that diet preferences of carp are not dependent on age. Because our juvenile carp were taken from experimental ponds stocked with *C. aspera*, *T. latifolia* and *Stuckenia* spp., prior feeding experience may have influenced their whole-plant feeding behaviour (Provenza *et al.*, 2003). All other assays involving agar-based pellets should not have been influenced by prior feeding experience and no change in consumption of pellets over the 3-day assays could be detected.

Although prior feeding experience should not have influenced this study, broc-let and commercial koi food may have subsidized diets, allowing higher ingestion of poor quality macrophytes. Herbivores require additional energy and protein to eliminate toxins (Provenza *et al.*, 2003). Therefore, supplemented koi food and/or broc-let, both higher energy sources than any of the macrophytes, may have enabled carp to consume more secondary compounds. Koi food had high levels of protein, fat, and fibre as well as other nutrients that may otherwise have been lacking in their daily diet. Results

may be conservative if the carp were able to consume more toxins due to a subsidized diet of koi and broc-let.

Terrestrial models of plant–herbivore interactions, such as the plant apparency and resource availability theories, both suggest phenolic chemical deterrents should be produced in significant quantities against generalist grazers in plants 'bound to be found' (Feeney, 1976) (although these patterns are not always consistent in terrestrial systems; Coley *et al.*, 1985; Bernays, 1989). However, the pattern in freshwater plants (our data) and marine plants (Hay & Fenical, 1988; Hay, 1991) does not fit predictions of the plant apparency model. The differences in defences may be due to macrophyte morphology such that emergent plants may be more defended structurally, while submergent plants may be more defended chemically. Carp differed in consumption of whole plant tissue of submergent (*C. aspera*, *S. pectinata*, *C. demersum*) and emergent (*T. latifolia*, *S. validus*) plants (*t*-test with d.f. = 78, $P < 0.001$), and carbon content was signifi-cantly higher in emergent than submergent plants as a whole (d.f. = 14, $P = 0.001$).

In cases where generalist herbivores occur at high densities relative to preferred food availability, they can drive food sources to local extinction (Hay, 1991), and this process can be exacerbated if the herbivore is exotic (Parker *et al.*, 2006). Carp cause lake-wide changes in water quality and macrophyte and macroinvertebrate abundance (Zambrano & Hinojosa-Garro, 1999; Miller 2006). Invasive generalist herbi-vores such as carp have direct and indirect effects on food web dynamics and community structure in aquatic ecosystems (Cronin, 1998; Stachowicz & Hay, 1999; Zambrano & Hinojosa-Garro, 1999; Miller 2006). Studies of feeding preferences help us to assess the direct impact of herbivores in freshwater commu-nities (Cronin & Hay, 1996c). This information is beneficial for predicting the impact of exotic species in aquatic ecosystems. Understanding the processes that influence macrophyte–herbivore interactions can help us anticipate the potential impacts of invasive gener-alist herbivores. Thus, studies of the importance of plant structure and chemistry and resultant suscepti-bility to herbivory can assist managers in choosing which macrophytes are appropriate for restoring areas impacted by herbivory. Specifically, this study suggests plants appropriate for increasing structural habitat in Utah Lake that may increase the probability for long-term recovery of the june sucker (Miller & Crowl, 2006). Thus, this paper is an example of how experiments that tie theory to application are import-ant for practical uses and for continued testing of theory.

Management recommendations

Since carp were introduced into Utah Lake, macro-phytes have been dramatically reduced and, in some cases, extirpated (*Ceratomphyllum demersum*). In this study carp had the highest consumption on *C. aspera*, which is now restricted only to inlets. *S. pectinata*, which is chemically defended, and *T. latifolia* and *S. validus*, which are structurally defended, still persist in the lake. Thus, we recommend restoring juvenile June sucker habitat with plantings of the emergent plants, *T. latifolia* and *S. validus*, and the submergent plant, *S. pectinata*, within Utah Lake. All of these plants are still found in the lake, although in lower densities than historically. Excluding adult carp (Miller & Crowl, 2006) with a mesh large enough for larval june sucker fish movement in areas where plants exist may increase the survival of the plants and provide june sucker habitat. Plants, such as *C. demersum*, may no longer be appropriate because they were unable to handle changes in lake chemistry after carp introductions. Carp negatively affect water quality (Parkos, Santucci & Wahl, 2003; Lougheed *et al.*, 2004), which should be taken into account when considering candidate plants.

Acknowledgments

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